

**Ecological response to sea level fluctuations in
the Upper Ordovician of Langesund, Norway**

M.Sc. Thesis by

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Acknowledgements

When Sir Arthur Conan Doyle lets his famous detective present himself in his first detective novel, “A Study in Scarlet”, he does that through a lecture in the art of deduction. He can enlighten Dr. Watson as well as the reader in how one from subtle clues like nails, face expression, scars and so on can draw conclusions about a person’s occupation. It is all about collecting thorough observations and from seemingly insignificant clues draw a picture that is hidden for the inexperienced eye. Everything is defined by the past, and inferring the links backwards gives an overview of a hidden truth. That is the basic science of Sherlock Holmes’ criminal inquiry.

This has been a challenging and an immensely interesting thesis to write, and I have discovered that invertebrate paleontology is great fun! I have felt a bit like the famous detective; collecting observations from a 450 million years old crime scene, analyzing and interpreting data to find the culprit; the “Doctor Moriarty” of species composition.

To help my inexperienced eyes to find and interpret the doctor’s subtle clues, I have received great help from my supervisors, Øyvind Hammer and Karl Inne Ugland. I must also mention the staff at the Geological Museum for their support, and especially David Bruton, Thomas Hansen, and his brother from the University in Tromsø, Jesper Hansen.

I will also mention my co-students, with whom I have discussed the facts and biology in general, and a special thank to Guri Sogn Andersen for proof reading of the manuscript. Thank you all for a fantastic social life. You have made my study worth the effort beyond the benefits of receiving a university degree. You have been of great biological inspiration, in disguise as music, guitar playing, cabin trips, camp fire, coffee, beer and colloquia. I am grateful for your support and all the fun we’ve had.

I was working on the proof of one of my poems
all the morning, and took out a comma. In the
afternoon I put it back again.

Oscar Wilde

1.0 Abstract

An upper Ordovician (upper Sandbian) benthic Paleozoic fauna at Langesund in the Oslo graben area has been reviewed. The study area consisted of the uppermost 13 meters of sediments in the Fossum Formation. A species/plot matrix retrieved in the formation has been analyzed with multivariate ordination techniques, extracting main gradients in species composition. The main gradient in species composition is correlated with sea level fluctuations already known. Results presented herein are interpreted as sea level fluctuations on a finer scale based on paleobiological evidence. Three fossil associations of importance are identified, with a decreasing abundance of primary producers correlated with increasing sea depths. The sea level fluctuation interpretation of a DCA ordination is supported by ecological assessment, including the abundance of primary producers, as well as the strength of the gradient, diversity patterns, occurrence of a superabundant culture of filter feeding *Leptæana* brachiopods, and a comparison of paleocurrents between lowstand and drowning events. These results are furthermore supported by sedimentological evidence.

2.0 Introduction

During the metazoan life history, beginning with the Ediacara fauna nearly 600 million years ago (Narbonne 2005), organisms have been forced to adapt to the changing face of the earth. The most challenging adaptations on a global scale must have been to survive the many extinction periods known from the fossil record (Futuyma 2005; Benton 2003). On the more local scale, adaptations to a changing environment, as from uniform tropic climates to undulating ice age/interstadial times in the Pleistocene (Barnes 2004), are a continuous challenge. Climate and other factors have affected the sea level which is a widely studied subject. Sea level changes of tens, and even hundreds of meters have not been unusual in a geological time perspective (Nielsen 2004; Hallam 1992). Such severe changes in the environment have influenced the distribution of species all along the fossil record until recent times. Organisms studied herein belong to an Upper Ordovician fauna around the Sandbian/Katian boundary, situated on the Baltic Craton. This craton today contains the areas of Scandinavia, Finland, Russia west of the Urals, the Baltic States and the northernmost part of Europe, leaving residues on Newfoundland after the Mesozoic break up of Pangea (Ziegler et al. 1977).

This paleoecological study was carried out in the Fossum Formation in Langesund, in the southwestern part of the Oslo Graben area. The Fossum Formation was described by Dahll (1857) and Owen et al. (1990), and has previously been subject to investigations of geological character. Thorough descriptions of the Oslo Region and the Langesund-Gjerpen area have been conducted by Størmer (1953) and Henningsmoen (1960). A new description and revision of Dahll's Fossum Complex (1857) was made by Harland (1978). He also renamed the upper calcareous part of the Fossum complex as the Steinvika Formation (Owen et al. 1990; Harland 1980). A mapping of the Langesund-Skien area was made by Inge Ribland Nilssen (1985). All of these studies contain mapping, logging and geological descriptions and they have given a solid framework for this paleoecological study.

I will examine species composition and diversity along gradients in a benthic Paleozoic fauna, and attempt relating these gradients in species composition to a set of dynamic abiotic factors, of which the most important are sea level and ocean currents. Sampling has been performed by collecting a species/plot dataset, consisting of 100 test squares and 17 species or taxonomic groups. Multivariate scaling techniques have been used to extract gradients, and some univariate statistical testing has been done for the purpose of understanding distribution and orientation of organisms. A small scale stratigraphic log has been recorded for comparisons with coenoclines discovered from the species/plot matrix, and to help the interpretation of environmental variables.

2.1 Main tasks of the study:

- Measure directions of *Leptaena* brachiopods and crinoid stems, to find information about ocean currents and fossils *in situ* properties.
- Retrieve a species/plot matrix.
- Extract coenoclines by the use of multidimensional scaling techniques and interpret results.
- Measure diversity indexes in the test squares in the species/plot matrix.
- Measure size of *Leptaena* brachiopods within and outside stratigraphical horizons with *Leptaena* superabundance.
- Retrieve a stratigraphical log on a small scale, as an abiotic support for interpretation of biogenous results.

3.0 Study area and geological setting

3.1 The Ordovician world

The study has been conducted in sediments deposited around the Sandbian-Katian boundary (middle Caradoc; Gradstein et al. 2004) in the Ordovician period. The study area was situated on the Baltic Craton. The Ordovician world was exceedingly different from the world we know today, both geographically and in other respects. Most landmasses were in the southern hemisphere, with the extensive Gondwana supercontinent placed around the South Pole. The Baltic Craton (Baltica) was situated around the 30° southern latitude (Cocks & Torsvik 2002). Three tectonic events may have affected the Baltic Craton at this time. The Taconic Orogeny was probably the largest tectonic event during this period, mostly affecting Laurentia (Cocks and Torsvik 2002; Rodgers 1971). The Avalonian Craton would soon collide with the Baltic, with some possible orogeny. Laurentia and Baltica were moving closer, beginning the Iapetus Ocean Closure and the later Caledonian Orogeny (Figure. 3.1) (Cocks and Torsvik 2002).

Prior to this, by the end of the late Precambrian, mountains made during the Sveconorwegian Orogeny some 1000 my ago had been peneplanated on the Baltic Craton. From the middle Cambrian and until the Caledonian Orogeny uplifted the continent above sea level during the Silurian and Devonian, the Baltic Craton was an epicontinental ocean area (Ribland Nilssen 1985). Sedimentation rates were low, probably in the absence of landmasses in the proximity.

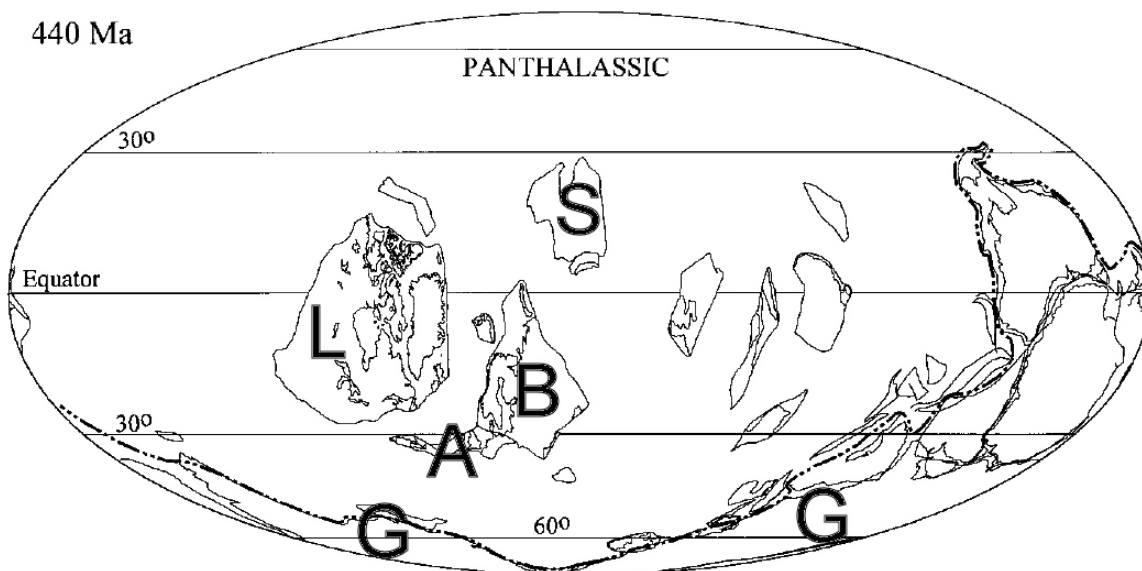


Figure 3.1: A map of the Ordovician world, as presented by Cocks & Torsvik (2002). First letters in names of cratons important for this study have been added, namely: Avalonia, Baltica, Gondwana, Laurentia and Siberia. The Iapetus Ocean is between the Baltica-Avalonia Continent and Laurentia. Avalonia did not collide with Baltica until after the Fossum formation was deposited.

Climatic and sea level change

Although the nature of Ordovician oceans and climates are poorly understood on a small scale, general trends in ocean levels and climatic conditions are quite well constrained (Barnes 2004). Due to atmospheric levels of carbon dioxide between 8 and 18 times recent levels, most of the Ordovician was in a high greenhouse stage. Ice caps were absent and climate was hot with wide tropical and warm temperate marine belts. The warm climate terminated in the End-Ordovician Ice Age, which has been associated with the End-Ordovician Extinction (Barnes 2004; Benton 2003). A decrease in carbon dioxide levels has been discovered during the latest part of Ordovician, towards the minimum in the late Ashgill (Barnes 2004).

Warm climate led to more sluggish ocean circulations, and warm water may have caused rigid and long lasting stratification of the ocean. Stratification of waters gives barriers for circulation, which again would lead to nutrient starved waters and oligotrophic conditions (Kaiser et al. 2005; Barnes 2004). The increased tendency for stratification due to warm climate, combined with an oxygen level 50% lower than the present atmospheric level, may have increased the tendency for anoxic conditions on the deep sea floor. Anoxic conditions in the deep sea may generate barriers, which would have an effect on fauna provincialism (Barnes 2004).

The Paleozoic has long been known for its significant variation in eustasy (Barnes 2004; Nielsen 2004; Hallam 1992), and the highest sea level known in the Phanerozoic is registered during the Caradoc (Hallam 1992). Most cratons were subject to extensive peneplanation, which gives less difference between land and sea floor, and thus an extensive flooding of continents, matching with the epicontinental ocean covering the Baltic Craton. The End Ordovician was characterized by changes in sea level, and in particular a regression during the Ashgill towards the end Ordovician ice age (Nielsen 2004; Hallam 1992). A shallowing has also been registered in the strata studied herein by Ribland Nilssen (1985) and Harland (1978).

Paleobiological setting

Except from the first plants which inhabited land during the early Llanvirn (Kenrick & Crane 1997), all known metazoan life in the Ordovician was marine (Futuyama 2005). However, the Ordovician is known for its great radiation of taxa that terminated in the End-Ordovician Extinction (Brenchley 2004). Ordovician strata are characterized by numerous fossils of organisms like brachiopods, trilobites, molluscs, conodonts among others. Taxa like blastoids, bryozoans, crinoids, corals and graptolites appeared for the first time in Ordovician tropical environments. The Cambrian/Ordovician boundary coincides with the first fossil appearance of pelagic graptolites, namely *Rhabdinopora* spp. (Gradstein et al. 2004). The time from the late Arenig to the Caradoc was the time of the greatest diversification of the most common brachiopods, with multiplying numbers of taxa many folds over a period of 20 million years. The superfamily *Strophomenoidea* radiated from one to 37 genera, and superfamily *Plectambonitoidea* from 17 to 43 genera (Cocks & Torsvik 2002), compared to only 325 known recent species of brachiopods.

Geological setting in the Oslo region

The Oslo Region is especially well suited for Paleozoic fauna studies due to its structural geology (Henningsmoen 1960; Størmer 1953). On the western parts of the Fennoscandian Shield, areas of Paleozoic sediments are trapped by faults due to Permian tectonic activity. Some of these faults have formed grabens, of which the Oslo Graben is by far the largest, forming a 220 km long structure within which Lower Paleozoic sedimentary rocks have been protected from erosion (Størmer 1953).

The area stretches from Langesund in the south and to Lake Mjøsa in the north, and is known for its rich Cambrian to Silurian deposits and Carboniferous to Permian igneous rocks; the latter which occupy most of the graben (Figure 3.2). The Lower Paleozoic succession is approximately 1400 meters thick, of which Ordovician sediments stand for about 450 meters. Sediments are often strongly folded. However, the successions in the Langesund-Skien area are not folded, but tilted eastwards by igneous activity and are cut by numerous faults. The same igneous activity has led to considerable metamorphism in some locations (Harland 1978; Størmer 1953). Metamorphosed sediments have been turned into firm siliciclastic and carbonate rocks resistant to erosion. Exposures in the area between Porsgrunn and Langesund are therefore generally good. Excellent exposures are found in the area around Steinvika and Langesundstangen, which makes this area very well suited for fossil community studies. The fossils are unfortunately considerably damaged by metamorphism during Permian magmatism (Harland 1978; Størmer 1953), but they are still good enough for paleoecological studies.

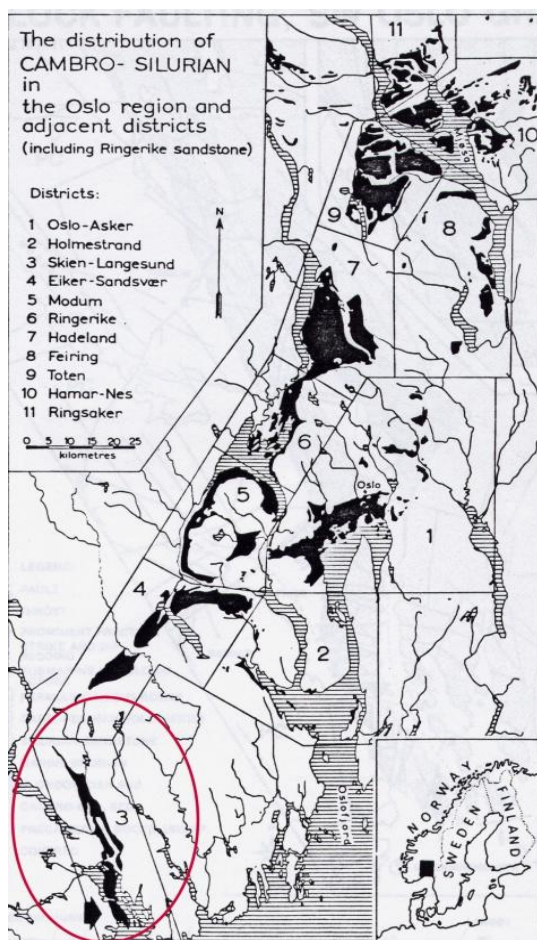


Figure 3.2: A map over the Oslo Graben area, shown relatively to the Norwegian map. Langesund is marked with an arrow in the red circle. The map is taken from Størmer (1957), with modifications.

3.2 Location

The Fossum Formation is a 255.5 meters thick formation, of which the Krogshavn Member represents the uppermost 109.7 meters (Ribland Nilssen 1985; Dahll 1857). The main part of this study concerns the top 14 meters of the Krogshavn Member in Steinvika, just below the base of the massive limestones of the Steinvika Formation. The Fossum Formation has been deposited over a time span of roughly 13.5 million years (Owen et al. 1990). This part of the formation has been deposited over approximately 740 000 years if sedimentation rates were constant. Some samples were also collected in Krogshavn, from sediments approximately 50 meters lower in the Fossum Formation.

All investigations have been performed in the excellent exposures in Steinvika and Krogshavn in Langesund, which is in the south western part of the Oslo Graben (Figure 3.2). Figure 3.3 illustrates the exact sampling areas in a small scale map over the study area with the two sampling localities marked with black squares.

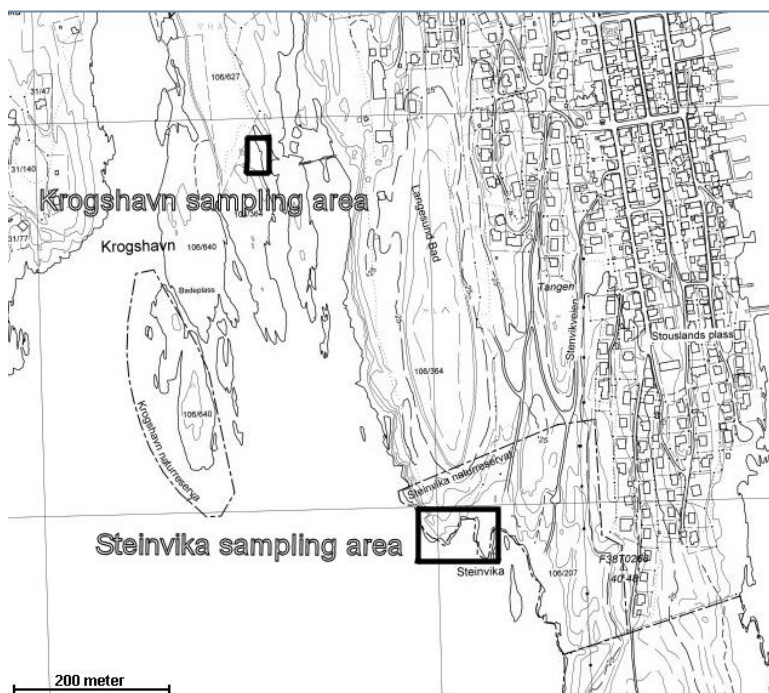


Figure 3.3: A local map of Langesund with sampling areas highlighted.

4.0 Material and methods

4.1 General information

All data were sampled in the vicinity of Langesund, as described in the “study area and geological setting” chapter. Due to geological protection of the area, all sampling was done by visual investigation of the rock in the field. Data were registered without bringing any samples to a lab or facilities better suited for investigation and photography than provided in the field. However, the quality of the fossils was good enough for a paleoecological study.

4.2 Processing of data

Data analysis was done with two different statistical utilities, namely the PAST and the R software package.

PAST (PAlaeontological STatistics) (Hammer & Harper 2001) is a free and easy-to-use data analysis package, and it constitutes a useful and effective statistical toolbox. PAST was originally developed for paleontological analysis, but is now a popular tool used in ecology and other fields as well. PAST is available at <http://folk.uio.no/ohammer/past/>.

R is a free integrated suite of software facilities for data manipulation, calculation, statistical analysis and graphical display. R is more complicated in use than PAST, but the package R is more flexible, and has got more possibilities than the PAST software. A large amount of extension scripts are available, helping the skilled user to perform almost any analysis desirable. R can be regarded as an implementation of the S-language which was developed at Bell Laboratories by Rick Becker, John Chambers and Allan Wilks (Becker et al. 1988). The R software and extensions are available at <http://cran.r-project.org/>.

Procedures

The study can be divided into four parts:

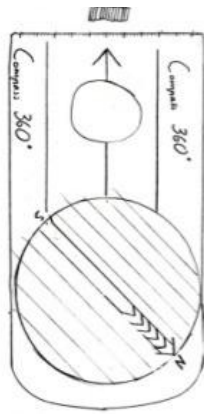
- 1 Investigating orientations of some superabundant fossils.
- 2 Collection and analysis of species composition data.
- 3 Investigating size composition of *Leptaena* brachiopods within and outside superabundant areas.
- 4 Retrieve a stratigraphic log.

4.3 Fossil orientation:

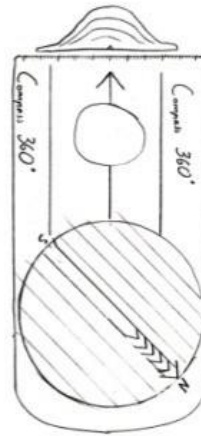
Orientations of 57 crinoid stems and 68 *Leptaena* brachiopods were measured using compass. Directions of brachiopods were measured as a normal angle to the hinge line. Orientations of Crinoid stems were measured normally to the stem length axis. Both methods are presented in Figure 4.1.

Figure 4.1: Orientation measurement. Method on *Crinoid* stems is illustrated to the left, and on *Leptaena* brachiopods is illustrated to the right.

Crinoid stem fragment



Leptaena brachiopod



The circular properties of directional data are not suitable for most statistical tests. The fact that 360 is close to 1 degree and opposite to 180 necessitates use of specialized statistical tests.

Directions were tested against uniform distribution using Rayleigh's test (Mardia 1972) for directional data in PAST, with geographical angle convention. Rayleigh's test has the following null and alternative hypothesis:

- H_0 : Distribution is uniform
- H_a : There is a single preferred direction.

Rayleigh's test is parametric, and assumes a von Mises distribution. Von Mises distribution is the circular equivalent to normal distribution. The test statistic parameter R is calculated with the use of trigonometric functions. This test is chosen because the distribution seems close to von Mises, and the alternative hypothesis of a preferred single direction is the most informative. An alternative approach would be the chi square statistic or the non parametric Rao's U test. The alternative hypothesis in these approaches is: Directions are not uniformly distributed. This approach does not give a preferred direction.

Leptaena brachiopods are distributed over 360°, while crinoid stems are distributed over 180°, as a result of their symmetry. *Leptaenas* are analyzed with 360° (unimodal) distribution, while crinoid stems are analyzed with a 180° (bimodal) distribution. In addition, *Leptaena* brachiopods are tested with 180° distribution for comparison with crinoid stems. In order to compare angular distribution of a crinoid stems, which is symmetric over two axes, with an angular distribution of a brachiopod that is symmetric over only one axis, the brachiopods must be presented as if the orientation around one

symmetry axis is arbitrary. *Leptaenas* are distributed over 180° in comparison with bimodally distributed crinoid stems, and a 360° unimodal distribution of leptaenas will not be suited for this comparison. Crinoid stems and *Leptaena* brachiopods have been tested for similar directions with the Watson-Williams test for equal mean angle in two samples (Mardia 1972).

Directional statistical methods are described in Hammer & Harper (2006) and Mardia (1972).

In addition to the circular orientation, *Leptaena* brachiopods were tested with a two-tailed binomial test for concavo/convex orientation. This was done in order to establish the preferred concavo/convex orientation of these brachiopods.

4.4 Species composition data

Information about species composition was collected within 100 squares (quadrats) of 0.25m² on the rock. Every fossil structure inside each square was recorded and identified to the taxonomic level possible given the quality of the fossils. Additional data to species composition was fossil preservation or quality, stratigraphic level, surrounding matrix and light conditions when registering. The stratigraphic level was estimated with a measuring tape, from the lowest level included in this study, 22 meters below the transition to the Steinvika Formation. The surrounding matrix was tested qualitatively for calcium carbonate with hydrochloric acid. Of this additional data, only stratigraphic level proved useful for further interpretations. Other information is therefore not presented further in the paper.

Forty of the squares were selected in areas with high fossil abundance. Sixty squares were collected semi-randomly with ten squares from six different shelves, or horizons in the rock. Location of the semi-random squares was determined by throwing a rock, and the place where this rock landed made the north-east corner of the square. Fossils were not numerous enough in semi randomly collected squares for separate analysis. The semi random squares therefore had to be included in the total species/plot matrix as described below.

Data from these investigations were collected into a species/plot (test squares) matrix, with species in columns and test squares in rows. Due to the properties of the DCA algorithm (the Decorana script by Hill and Gauch 1980), orientation of matrix into rows and columns may affect length of gradients and is therefore important (Hammer & Harper 2006).

Fossils were not found in all squares, and only the 67 test squares with registered fossils were used for analysis.

The species/plot dataset was analyzed with multidimensional scaling methods to extract main gradients of change. Dissimilarities in species composition between test squares can be presented as distances between objects (test squares) in a diagram. Objects are rows in the matrix, and the distance refers to species composition. If one attempts to plot four different objects with equal distance in a two-dimensional diagram, it is obvious that it is impossible to get the same distance between all objects. A third dimension must be used. This approach gives us one new dimension for each new object (e.g. row in matrix), and often many more than three. A complex multidimensional space is difficult to interpret.

Multidimensional scaling techniques simply estimate the projection in the multidimensional space that visualizes maximum change in a minimum number of dimensions. The ordination diagram will

then ordinate test squares with similar species composition close together, and test squares with increasing difference in species composition with increasing distance.

Extracting such gradients of change in a species/plot dataset is a difficult task, due to the properties of the dataset. Nonlinear effects like the arch effect are often found in results (Jongman et al. 1995; Økland 1990). One must therefore pick methods with care, and preferably use two different methods for comparison, in order to get more confidence in the results.

The methods chosen for the present study were Detrended Correspondence Analysis (DCA), and Non Metric Multidimensional Scaling (NMDS).

The DCA is a modified Correspondence analysis (Hirschfield 1935). The Correspondence analysis estimates species modes by weighted averaging regression. Dimensions are calculated by a regression and calibration iteration procedure towards convergence, a procedure called reciprocal averaging. This ordination often presents the largest gradient of change as an arch. In DCA the detrending algorithm straightens out this arch. The specific DCA algorithm used herein is based on the Decorana script by Hill and Gauch (1980).

NMDS is a heuristic algorithm by Kruskal (1964). The algorithm tries to fit the data as well as possible, on the basis of a distance matrix made from the species/plot matrix. Bray-Curtis distance measurements were considered to be ideal, due to its built in normalizing feature. Distance measures take values between 0 and 1. Misfit to the distance matrix will be displayed as a stress value. Due to the problems of being trapped in local optima, this procedure needs to be done several times, and the ordination with the lowest stress value is used. NMDS was replicated 200 times. The specific NMDS algorithm used herein is the Global Non metric Multidimensional Scaling (GNMDS) in R.

Results from the GNMDS and DCA analyses were compared with a Kendall's tau correlation test (Kendall 1938) and Procrustes test of complete ordinations (Schönemann & Carroll 1970). Multidimensional scaling techniques and comparisons are thoroughly described in Hammer & Harper (2006), Jongman et al. (1995), and Økland (1990).

Both PAST and R were used for ordination methods and correlation between them.

4.5 *Leptaena* size composition

Leptaena brachiopods are among the most abundant organisms in the study area. They are superabundant and appear in nearly monoculture in an approximately 20 cm thick zone. They are abundant also at other levels, but not to the same extent.

The length from the center of the hinge line to the anterior margin of the commissure was measured, both within and outside areas of superabundance. This was conducted for comparison between *Leptaena* from superabundant areas and elsewhere, in order to understand the ecological properties of the *Leptaena* monoculture.

Results were tested for different mean size with a Student's *T*-test and different variance with an *F* test.

4.6 Stratigraphic log and testing

A logistic regression has been used to recognize a trend in the thickness of the alternating mudstone/siltstone beds. Lithological types have been given the values 0 or 1 for each cm ordered stratigraphically. Increasing thickness in sediments will then be presented by longer series of one of the categories, 0 or 1, and shorter if the thickness is decreasing. A logistic regression has been performed to test for trends in the relationship between siltstones and mudstones. The regression has been performed as a GLM with family=binominal in R.

5.0 Results

5.1 General results from fossil collection

A total of 2373 fossils or fragments of fossils were registered during fieldwork. 1280 were registered in 40 test squares selected by fossil abundance, and 386 in 60 semi-random test squares in the Steinvika section. 279 fossils were registered in a lower stratigraphical section at Krogshavn, from six test squares selected by fossil abundance. This gives a total of 1945 fossils in the species/plot matrix. The six test squares from the lower section were between 49 and 50 meters below the upper section. No stratigraphy has been recorded in the lower section, other than registering the level. In addition to the species plot matrix, 428 *Leptaena* brachiopods and crinoid fragments were registered for analyses of direction and size distribution. Some of the fossils registered for direction and size might also be registered in the species plot matrix. Fossils from all 106 test squares are registered in Table 5.1. Fossils are identified to different taxonomic levels, into 17 different groups. Presence of the trace fossil *Chondrites* was also registered on 20 of the test squares. Abundance of fossils relative to stratigraphic level is presented as a spindle diagram (Figure 5.1). The identified taxonomic groups are presented in Appendix 1. *Chondrites* are difficult to include in ordinations. *Chondrites* are therefore not included in any analysis, and are not further included in this study.

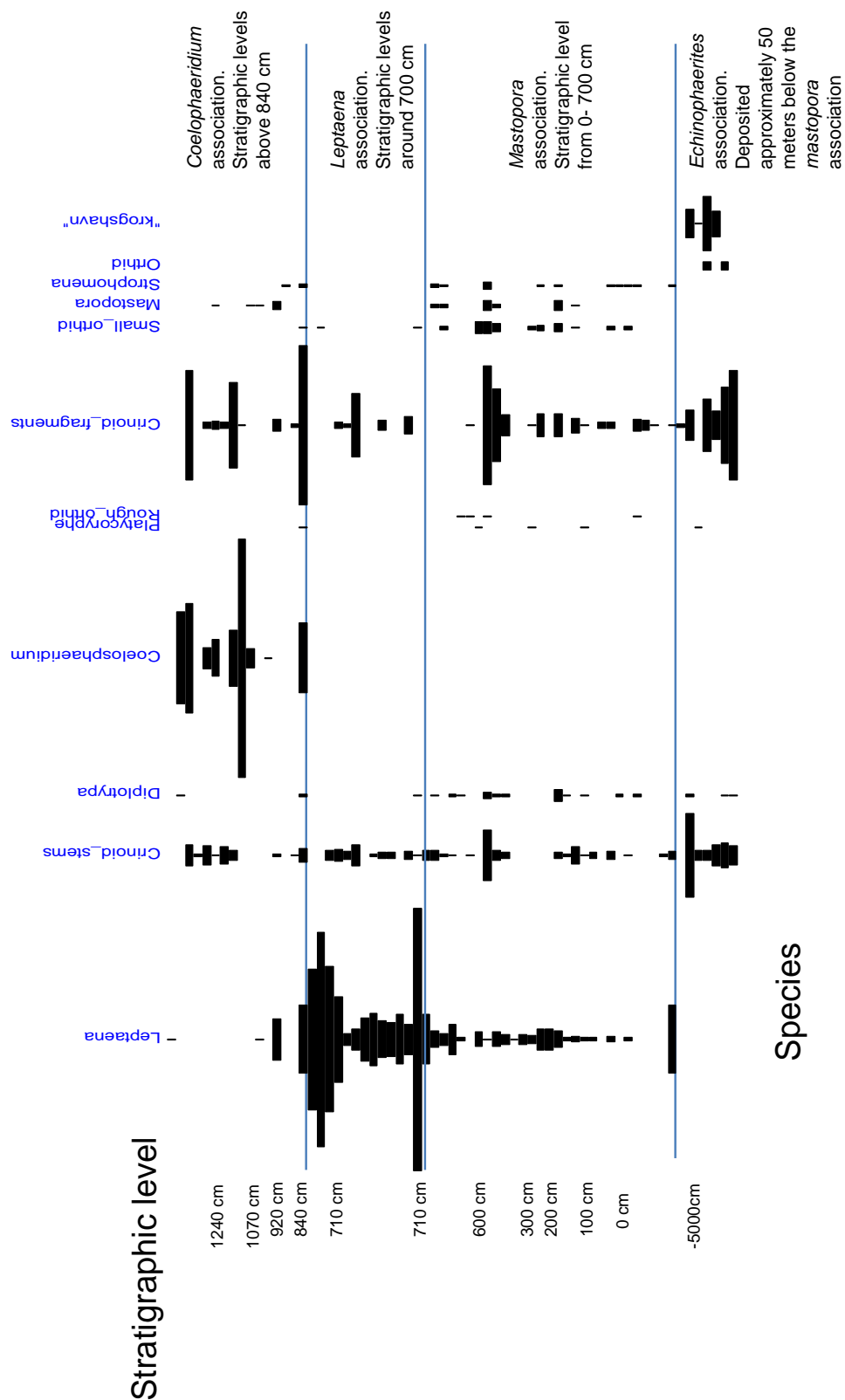


Figure 5.1: Spindle diagram showing distribution relative to stratigraphic level. The width of the columns shows abundance. Values on the Y axis show relative stratigraphic level. Y-values are not scaled, and do not show stratigraphic distance between test squares. Four associations are identified and described in the left of the figure.

Table 5.1: Abundance of species in 60 semi-random, 40 selected test squares, and 6 test squares from the lower section.

Species	Random squares	Selected squares	Lower section	Sum
<i>?Chasmops</i>	0	2	0	2
<i>Coelosphaeridium</i>	10	285	0	295
Conulariida	0	1	0	1
Crinoid fragment	41	336	136	377
Crinoid stems	28	128	79	156
<i>Diplotrypa</i>	1	25	0	26
<i>Diplotrypa</i> , large	0	0	4	0
<i>Echinosphaerites</i>	0	0	51	0
Gastropod	0	2	0	2
<i>Strophomena</i>	3	14	0	17
<i>Leptaena</i>	292	431	0	723
"Krogshavn" orthid	0	0	8	0
<i>Mastopora</i>	2	22	0	24
<i>?Ogygiocaris</i>	0	1	0	1
<i>Platycoryphe</i>	1	4	1	5
Rough orthid	0	2	0	2
Small orthid	8	27	0	35
Total	386	1280	279	1945

5.2 Directional analysis of fossils.

Directional analysis of *Leptaena* brachiopods and Crinoid stems.

Directions of 68 *Leptaena* brachiopods and 57 crinoid stems were measured normally on the hinge line or normally to the crinoid stem orientation. Directional histograms were retrieved from PAST, and both *Leptaena* and crinoid directions deviated significantly from a random distribution (Table 5.2), using Rayleigh's test. It is visually obvious from diagrams in Figure 5.2 that *Leptaena* brachiopods are unimodally distributed, and that a von Mises distribution model is appropriate. Crinoid stems have a symmetric bimodal distribution over 360°, which is equivalent to a unimodal distribution over 180°. The bimodal orientation of brachiopods is presented for comparison with crinoid stem orientation. In order to compare an angular distribution of a crinoid stem which is symmetric over two axes with an angular distribution of a brachiopod that is symmetric over only one axis, the brachiopod must be presented as if the orientation around one symmetry axis is arbitrary. Bimodal crinoid orientation and bimodal *Leptaena* orientation were tested with the Watson-Williams-test in the PAST package. The test could not determine any differences between the two orientations ($p=0.976$).

Table 5.2: Data retrieved from directional analysis

Graph	Species	Mode	Mean	$p(\text{rand})$
1	<i>Leptaena</i>	Unimodal	57.32	8.64×10^{-8}
2	<i>Leptaena</i>	Bimodal	55.58	5.67×10^{-4}
3	Crinoid stems	Bimodal	55.23	5.14×10^{-2}

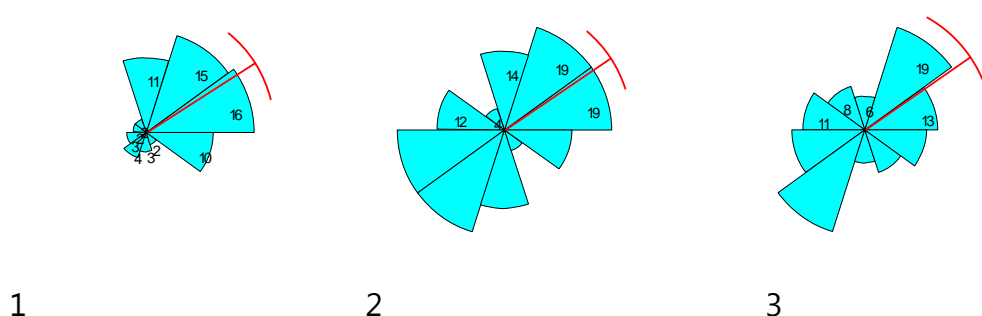


Figure 5.2: Directional histograms with angular mean and its 95% confidence interval as a red line. 1) Shows *Leptaena* with unimodal distribution, 2) shows *Leptaena* orientation with bimodal distribution, and 3) shows crinoid stem orientation, with bimodal distribution.

Concavo-convex orientation of *Leptaena* brachiopods

Concavo-convex orientation of 188 *Leptaena* brachiopods was measured, with a distribution as presented in Table 5.3. Only six percent of the brachiopods are registered with the convex side facing down, which must be considered as a deviation. A two-tailed binominal test established the higher frequency of registrations with the convex side up as highly significant ($p < 0.001$).

Table 5.3: Concavo-convex distribution of *Leptaena* brachiopods.

<i>Leptaena</i> convex side orientation		
	Counts	Percent
Down	11	5.85
Up	177	94.15
Total	188	100

5.3 Ordination of the species/plot matrix

Plots from the lower stratigraphical section collected in the Krogshavn sampling area contained crinoid stems and fragments, *Echinosphaerites*, a kind of orthid brachiopod (here named the “Krogshavn orthid”), and *Diplotrypa*. *Diplotrypa* colonies from the lower section were expressed differently than in the upper section. The colonies were between 5 and 10 cm in diameter, as opposed to in the upper part where colonies were between 1 and 2 cm in diameter. The two colony types are treated as two distinct “species” or fossil groups.

Apart from the crinoid stems, the species compositions in the six plots from the lower section were completely non-overlapping with the species composition in the upper section. They were therefore not suited for multivariate analyses and have been excluded. The species/plot matrix consisted of 59 test squares after discarding non-informative test squares and test squares from the lower section (species plot matrix with is presented in appendix3).

A DCA analysis of the species/plot matrix was retrieved with eigenvalues and axis lengths as presented in Table 5.4. The DCA ordination diagram is presented in Figure 5.3.

Gradients are measured in Hill's scaling, which is equal to standard deviations. Four units on Hill's scaling represents approximately one complete species turnover. The length of the first DCA-axis is 3.4, and represents a clear gradient in species composition.

Polygons have been drawn around four groups of fossils. The red polygon represents test squares with *Leptaena* superabundance and no primary producers. The blue polygon contains test squares with *Mastopora* primary producers and the light green contains test squares with *Coelosphaeridium* primary producers in addition to some *Mastopora*. These groups are here named the *Leptaena* association, the *Mastopora* association and the *Coelosphaeridium* association. The dark green

polygon contains test squares with none of the species in the other three groups. The *Leptaena*, *Mastopora* and *Coelosphaeridium* associations are distinct groups, and they arrange respectively from low DCA values to high DCA values. A fourth (*Echinosphaerites*) association was identified in the Krogshavn sampling area. This part of the dataset was not meaningful in ordinations and is not presented in further ordinations.

Table 5.4: DCA ordination data

	DCA 1	DCA2	DCA3
Eigenvalues	0.756	0.177	0.153
Axis lengths	3.40	1.99	2.27

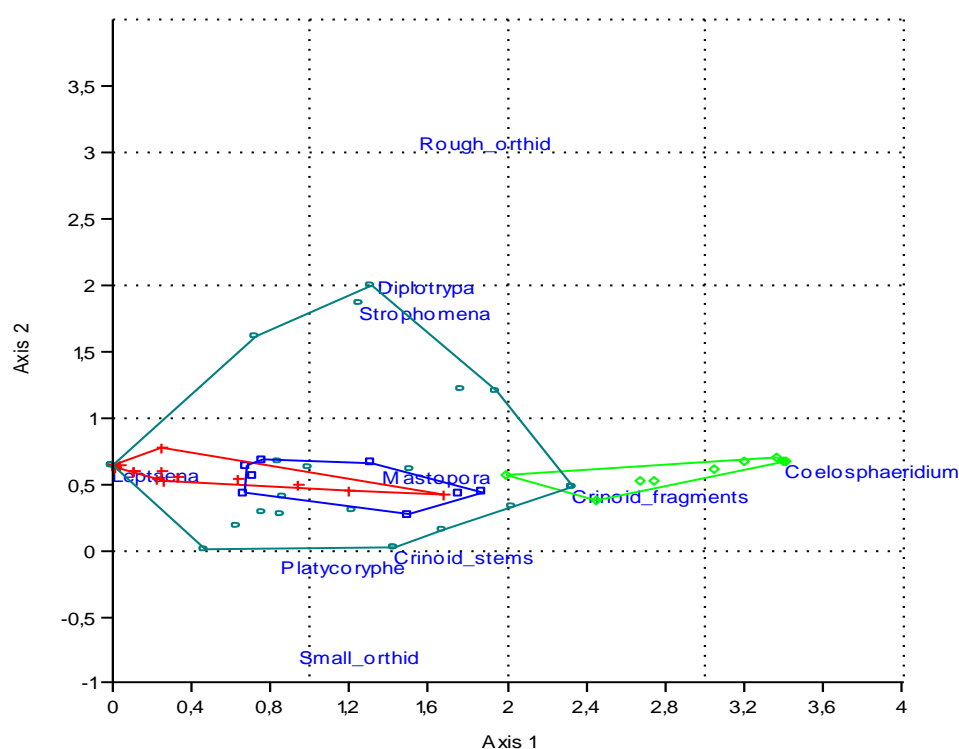


Figure 5.3: DCA ordination of the species/square matrix, plotted with square scores as coloured dots and species scores as text labels. Red polygon outlines the *Leptaena* association, blue outlines the *Mastopora* association and light green outlines the *Coelosphaeridium* association. The dark gray outlines test squares that did not fit into other groups. The first axis explains a 4.3 times larger portion than the second axis.

Additional ordination and comparisons

In addition to the DCA ordination, a GNMDS ordination was performed for comparison, in order to get confidence in the DCA gradients. The GNMDS diagram with Bray-Curtis dissimilarity measure is presented in Figure 5.4. The ordination returned a stress value of 20.56. As presented in Figure 5.5, the GNMDS analysis returned a scattered Shepard plot, which points to some inconsistency between dissimilarity matrix and the ordination diagram.

The DCA and GNMDS ordinations were compared by the use of Kendall's tau rank correlation test for the first axis, giving $p < 0.001$ and a Kendall's τ of 0.42, which indicates a good correlation.

To get a visual idea of the correlation between ordinations, a Procrustes analysis of complete ordinations was also performed. The analysis returned the diagram presented in Figure 5.6. The Procrustes fit gives a good visual impression of the differences between the two ordinations, showing that most errors are on the second ordination axis. The first dimensions in the two ordinations are strongly correlated.

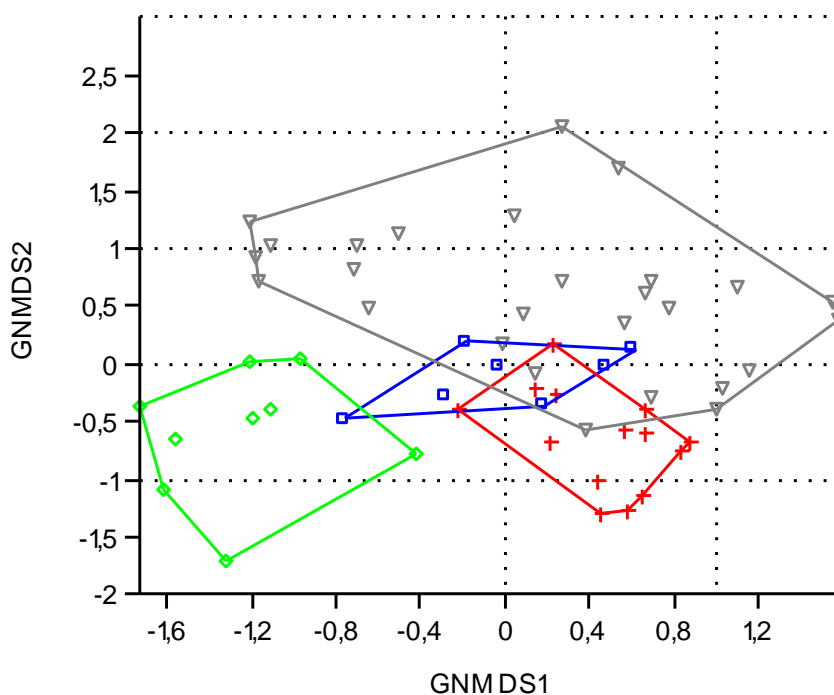


Figure 5.4: The GNMDS ordination diagram. Stress value is 20.56. Red polygon outlines the *Leptaena* association, blue outlines the *Mastopora* association and light green outlines the *Coelosphaeridium* association. The dark green outlines test squares that did not fit into the other groups. The ordination performed in R and plotted in PAST

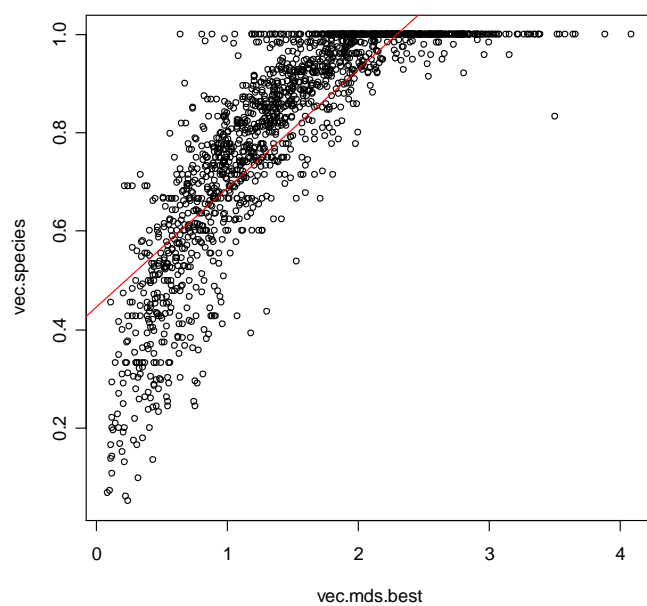


Figure 5.5: Shepard plot from GNMDS ordination. The diagram is scattered, indicating some deviation between the distance matrix and the ordination plot.

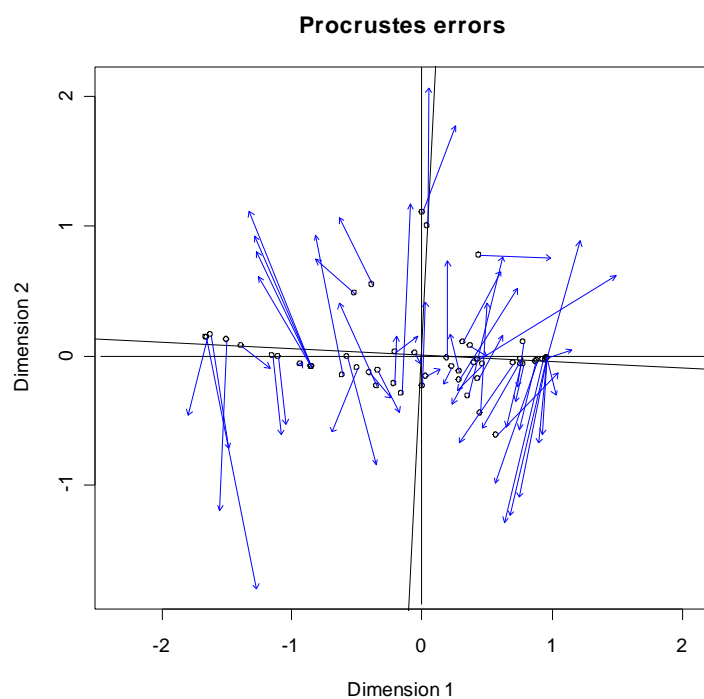


Figure 5.6: Procrustes comparison between the GNMDS and the DCA. Most of the deviation is on the second axis. This analysis gives us much confidence in the first dimension of the ordination.

5.4 Analysis for interpretation of ordinations.

The DCA scores were used further in the two following analyses in order to interpret the ordinations.

Plot of DCA1 values against stratigraphic level.

DCA1 values plotted against stratigraphic level (relative time) reveals a non-linear relationship between the species composition gradient and the stratigraphic level (Figure 5.7). The DCA scores drop towards the stratigraphic level of 600 cm, and then increase again. The smoothing curve is made with the B-spline fit function in PAST (10 decimates).

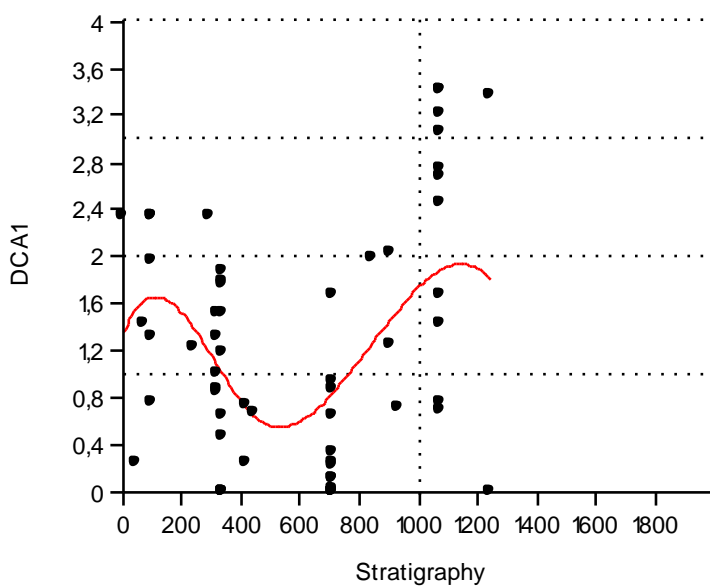


Figure 5.7: Stratigraphic level plotted against ordination axis values. The red line is a centre line to illustrate the mean relationship between stratigraphic level and the ordination values. The red line is not a perfect fit and is displaced slightly to the left. This overshooting is a result of the sparse amount of data in the stratigraphic levels between 400 and 600. The lowest mean DCA-values should be at ca 710 cm, in the *Leptaena* association.

Plot of DCA1 values against fisher-alpha diversity index.

A plot was made of the DCA scores against the Fisher-Alpha diversity index. Species diversity shows a peak at DCA value 0.8, in the transition between the *Leptaena* association and the *Mastopora* association. The plot is presented in Figure 5.8.

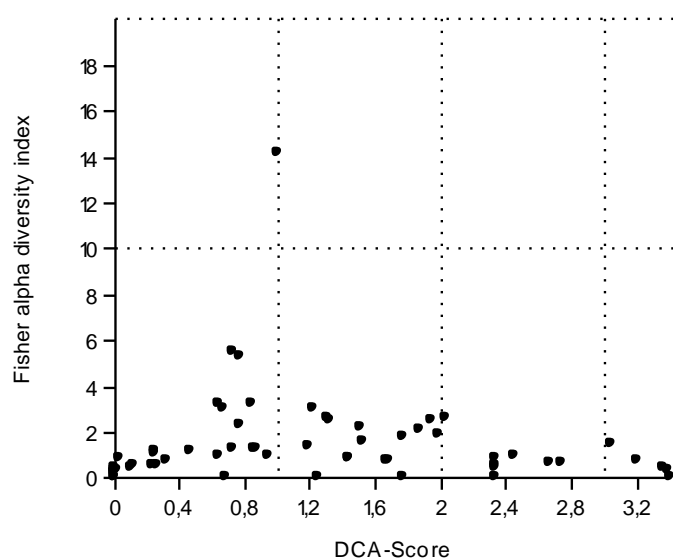


Figure 5.8: DCA plot scores on axis one plotted against The Fisher-Alpha diversity index.

Plot of DCA1 values against number of primary producers

A plot was made of DCA1 values against the number of primary producers. The amount of primary producers increased correspondingly with increasing DCA1 values, as presented in figure 5.9. The amount of primary producers especially increases in the *Coelospharidium* association.

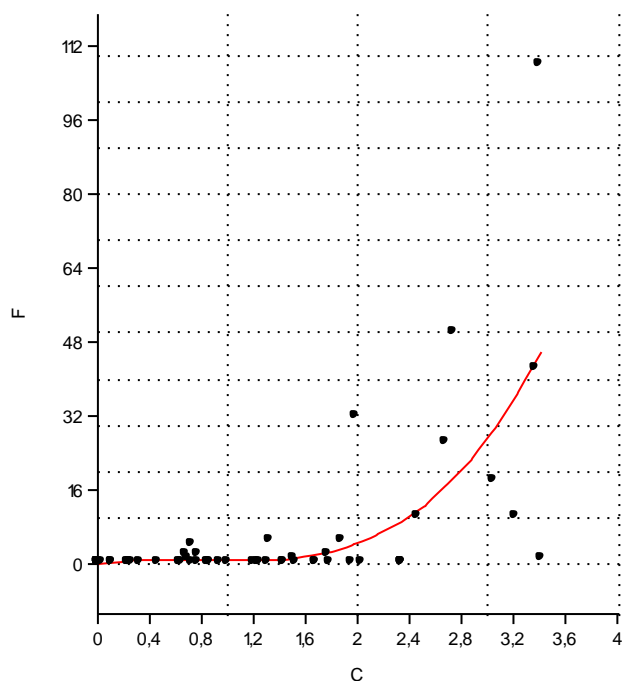


Figure 5.9: Plot of primary producers against DCA1 values. The amount of primary producers increases with increasing DCA1 values. The smoothing curve is made with a 3. degree polynomial fit in PAST, and is not tested statistically.

5.5 Size composition of *Leptaena* brachiopods in monoculture and elsewhere.

75 *Leptaena* brachiopods from the *Leptaena* association and 40 from elsewhere were measured in length and width. Comparison of the two groups displays a variation between them. Statistical data are presented in Table 5.5. Width of *Leptenas* was not measured due to fossil quality. Both size and variance differ significantly. *Leptaena* size distribution in respective groups is presented as histograms in Figure 5.10 and Figure 5.11.

Table 5.5: Statistics of *Leptaena* comparisons. The superabundant (*Leptaena* association) and background (elsewhere) groups differ significantly in both size and variance.

	Length	
	<i>Leptaena</i> association	Elsewhere
N	75	40
Mean	11,36	9,55
Variance	0,65	2,45
		P(same)
F (variance)	3,81	7,48E-008
T (mean)	-8,2	4,26E-013

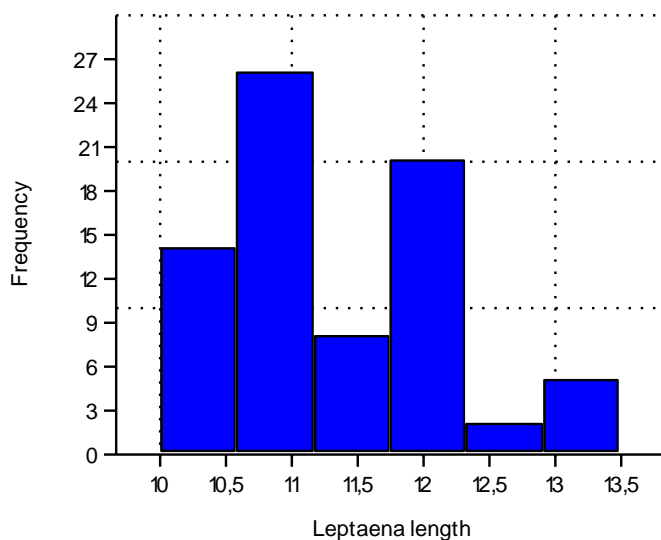


Figure 5.10: Histogram of *Leptaena* size distribution inside the superabundant areas. The diagram shows a prominent bimodal peak.

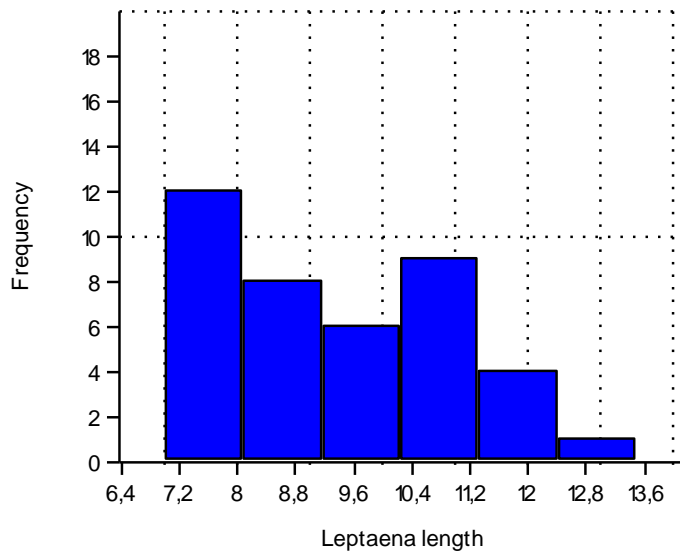


Figure 5.11: Histogram over Leptaena size distribution in the background areas. The bimodal peak is less prominent than in Figure 5.10.

5.6 Stratigraphic results

In total 1292 centimetres of sediments was logged in detail at 1:5 scales. The lower six meters consisted of siliciclastic mudstones and siltstones in an alternating pattern. The uppermost part consisted of some bioclastic calcareous sediments, in which the alternating system is absent. A cyclostratigraphic analysis was performed, but results from this analysis did not fit into the context of this paper. This analysis is therefore briefly presented in the appendix. The total stratigraphic log is presented in Appendix 2.

Thickness of alternating layers

The lower six meters with a distinct alternating pattern showed a decreasing trend (decrease in siltstone relative to mudstone). The trend is most distinct from approximately 100cm to 600 cm, as presented in Figure 5.12.

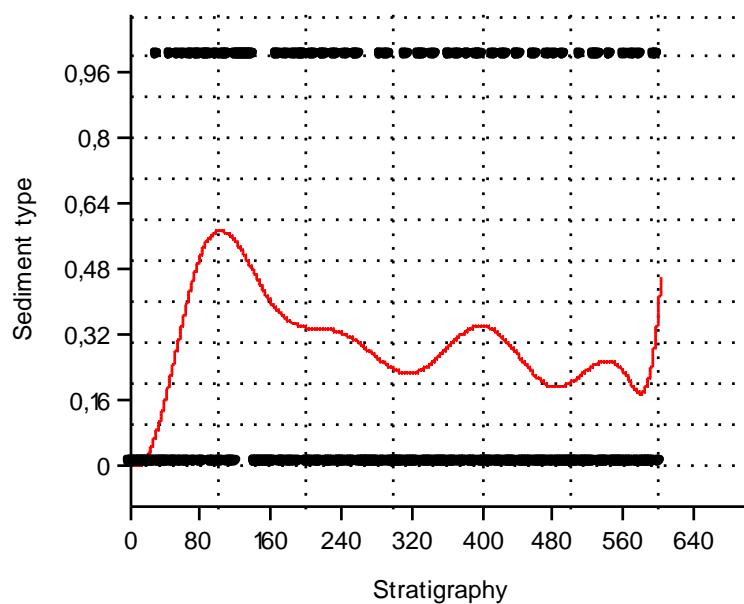


Figure 5.12: B-spline fit, with 80 decimates. Each dot with the value of 1 in the diagram represents one cm in the sediment composed by siltstones, while the value 0 represents each cm composed by mudstone. The red line shows a decreasing trend in elements of siltstones in the sediments from 100 cm to 600 cm.

A logistic regression on alternating beds in the sediment was performed in R. The test was performed on stratigraphic levels from 100 cm to 600 cm in the upper section, to test for trends in thickness of siltstone beds. The test returned a significant decreasing trend in siltstone proportion. $p=0.001$ (Figure 5.13).

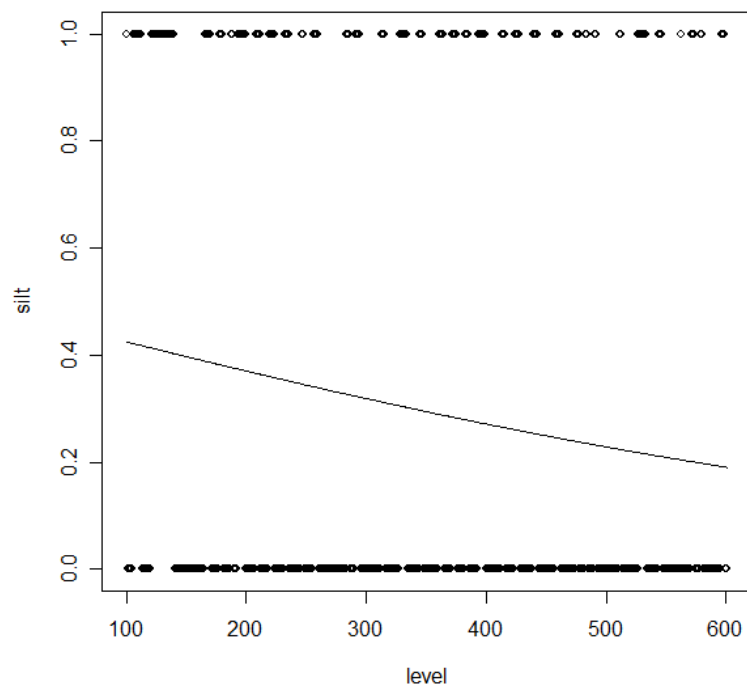


Figure 5.13: The logistic regression, returning a downwards trend over the stratigraphic levels from 100-600cm.

6.0 Discussion

6.1 Methodology

Post mortem community disarrangement

In paleoecological studies it is usually very difficult to assess the spatial distribution of local species assemblages. Fossils may be transported *post mortem* by paleocurrents, turbiditic flows or bioturbation that disarrange assemblages. Results here are based on the organism's properties when they were alive, and considerable effort has therefore been made considering whether fossils are preserved *in situ*.

Of all the fossils registered in this study, *Leptaena* brachiopods and crinoid stems are the organisms best suited for study of *in situ* properties. This is because they are distributed all through the stratigraphy of the study area, and because they are numerous, which makes the data well suited for statistical analyses.

In addition to the biological evidence, sedimentation patterns provide clues of taphonomy and transport. Alternating sediments in the Fossum formation are interpreted as fine sediments from easy waters interrupted by more coarse sediments from storms (Ribland Nilssen 1985). The intuitive conclusion is thus that fossils found in fine sediments are not transported. Most fossils registered, except *Chondrites* are found in fine sediments. However, directional analysis of both *Leptaena* and crinoids (Table 5.3; Figure 5.2) indicates a unidirectional current. Two questions arise from this discovery: Have organisms moved themselves in beneficial orientation for filtration, or have they been moved by the current *post mortem*? In the latter case, has the *post mortem* transportation been extensive?

Both laboratory and field studies of crinoids *post mortem* point to rapid decay and disarticulation (Maples and Archer 1989; Meyer and Meyer 1986). Disarticulation in recent comatulid crinoids (feather stars) is even known to start before death (Meyer and Meyer 1986), but how this will be expressed in non-comatulid crinoids is not mentioned. Spectacular preservation of crinoids with intact calyx, pinnules and arms is often interpreted as a result of rapid burial (Maples and Archer 1989). Crinoids here are only found as relatively small debris, with an exception of a 40cm long crinoid stem. The observed orientation of these fossils must therefore have occurred *post mortem* and some *post mortem* transportation must have taken place. Schwarzacher (1963) has investigated patterns made by artificial crinoid debris in a laboratory experiment, resulting in complex patterns of orientations. However, his main conclusion is that crinoid debris is oriented parallel to the current if the current is strong; and perpendicular to the current if the current is slower. The occurrence of a 40 cm long crinoid stem in the same layer as the measured crinoid debris precludes rough waters during the time between decay and burial. Since only the stem, and not the calyx, pinnules or arms are preserved, the preservation of this stem cannot be regarded as evidence of rapid burial, but rather as evidence of little movement of the waters. It is therefore reasonable to conclude that crinoid stems have not been moved far from their place of death. They are thus probably oriented perpendicular to the current.

Life position of *Leptaena* brachiopods has been a subject of debate for decades, and many papers are published on this theme. The old paradigm is that *Leptaena* lived partly buried in the soft sediments with its convex side facing down, extending its commissure above the sediment to access the water for filter feeding (Hoel 2008; Lescinsky 1995). The main problem with this interpretation is that most leptaenas are found with the convex side up (Hoel 2008; Lescinsky 1995), which is also the case in the present study. On the contrary, Lescinsky (1995) argues for a life position with the convex side up, based on presence of epifauna, interpreted to have inhabited the brachiopod when it was alive. Most epifauna are on the convex side of the shell. Lescinsky does not explain how the organism can feed with the commissure buried in the mud. Hoel (2008) argues for a vertical life position. *Leptaena* anchored itself to the sediments with its pedicle, with the convex valve facing the current. Morphological features of the shell are interpreted as muscular attachments for lowering and hoisting the shell vertically, positioning itself ideally for filtering water. The characteristic morphology of the commissure leads to an increased turbulence in this position, transporting more water over the lophophore. After the brachiopod is dead, the pedicle no longer supports the vertical position. The *Leptaena* falls over, and with the current pushing on the convex valve, it tips over with the convex valve facing up. The position with convex valve facing up might therefore be as close as it gets to the *in situ* position of *Leptaena*. With the convex side facing the current, some sediment might be trapped in the back eddy, making the concave side uninhabitable for filter feeding epifauna. A vertical life position is then also consistent with the findings of Lescinsky (1995).

Even though the convex-up might be the *in situ* position of *Leptaena*, this preservation may also occur since this is the most hydrodynamic stable position. If that is true, leptaenas transported by currents would probably have a distribution with the lion's share in this position. A strong current would also orient organisms directionally. However, the *Leptaena* brachiopods in the Krogshavn member are strongly unimodally oriented (Figure 5.2). If they were oriented *post mortem*, a 180° orientation would be anticipated, and orientation around the center line would be arbitrary. In situ studies show that recent brachiopods orient their commissure perpendicular to the water current. Experiments have even shown that some (but not all) species have the ability to actively turn around the pedicle by muscular actions (Alexander 1986; LaBarbera 1977 & 1978). The unimodal directional orientation, the fine sediments and the occurrence of a 40 cm crinoid stem strongly supports an *in situ* orientation.

The direction of the length axis of brachiopods is perpendicular to the crinoid stem length axis (Table 5.3; Figure 5.2) when methods used for measuring directions are considered. Both the sedimentology, the distribution of the two groups of fossils, and the occurrence of one 40cm long crinoid stem, indicate that they have been exposed to a slow current. Following from this deduction is not only that the organisms probably are *in situ* distributed; it also presents a clue of direction of the main current. Current directions will be further discussed later in the discussion chapter.

The study area is interpreted to be deposited at different depths. Crinoid fragments registered in sediments deposited during a lowstand period are more fragmented and possibly subject to higher energy waters. A larger amount of allochthonous elements could be present in lowstand sediments. However, since this may be considered as a function of sea level fluctuations, it is still safe to conclude that the data is well suited for this ecological study.

Multivariate methods and the ecological niche concept

An environmental variable could be considered as a gradient in which each species has got a niche that satisfies its environmental requirements (Økland 1990; Whittaker 1973). Two of these gradients will then compose a two-dimensional variable system, or an area of requirements; three makes a volume. The species total set of requirements is referred to as the n-dimensional hypervolume, or as its fundamental niche (Whittaker 1973; Hutchinson 1957). If all variables, both physical and biological could be described, the fundamental niches of any species will completely define their ecological properties (Hutchinson 1957).

A species does not usually fill its fundamental niche. While the total set of requirements constitutes the fundamental niche, the set of requirements actually used is the realized niche.

The realized niche consists of intervals along gradients of environmental factors in a multidimensional hypervolume. The counterpart of the environmental niche concept is the species composition response to environmental variables. Species will organize themselves in the n-dimensional environmental variable hypervolume complementary to their environmental requirements. Extraction of gradients of community change, or coenoclines (Økland 1990; Whittaker 1973) from the species composition hypervolume, may be useful in understanding and visualizing gradients of maximal change in species composition.

These gradients may be used to interpret environmental data, and are valuable in understanding the paleobiological environment as well as recent ecology. Extractions of complex gradients from a community are multidimensional problems, and the use of complex multidimensional scaling techniques are required.

Detrended correspondence analysis and non metric multidimensional scaling

Detrended Correspondence Analysis (DCA) is a controversial method, due to the somewhat ad hoc removal of the arch effect by the detrending algorithm. A usual distortion in the result is the tongue effect, which may affect the second DCA axis. The first axis is only affected by the non-linear rescaling, which is a robust calculation (Økland 1990). A tongue-shaped diagram might also reflect a real structure of the data. Due to the weaknesses of DCA, results from this analysis have been compared with Global Non metric Multi Dimensional Scaling (GNMDS). The Kendall's τ rank correlation test of the first axis in DCA and GNMDS ordinations is highly significant ($p < 0.001$); a comparison which gives the first ordination axis confidence. The DCA diagram is presented in Figure 5.3. There seems to be a tongue effect in the GNMDS diagram (Figure 5.4), but since the second axis will not be interpreted further, that will not be considered as a problem. A Procrustes test visualizes the differences between the two ordination methods including the arch effect (Figure 5.6). Most deviations are related to the second axis. I conclude that DCA1 reflects a real gradient, and DCA1 may be used for further interpretations.

Unfortunately DCA and the Decorana script do not return a total inertia, and eigenvalues as percentages of the total inertia are not presented (Oksanen pers. comm.). However, the eigenvalue on the first axis is 4.3 times larger than on the second axis. The first axis must represent a very strong component of species composition. The GNMDS analysis performed here did not give a dense Shepard plot (Figure 5.5), and GNMDS does not necessarily present one single axis of maximal variation. It is therefore not the best suited for further analysis. DCA values rather than values from

GNMDS have been used for further analysis because the first axis in a DCA ordination is robust; it presents one single axis of maximal variation and gives a good foundation for comparison with other research. DCA is widely used in paleontological research (E.G. Brett et al. 2007; Botquelen et al. 2006; Scarponi and Kowalewski 2004; Holland et al. 2001). Other axes from ordinations will not be interpreted.

Relationship between DCA and environmental factors

Gradients in species composition retrieved from ordinations are the species response to a change in environments. From the environmental point of view it is a complex gradient. The gradient represents co-variation between many environmental variables. A more extensive change in one environmental variable will increase its impact on the species composition gradient, and thereby increase the eigenvalue on the axis on which it has most impact. It will also represent a larger portion of the eigenvalues in the species/plot ordination.

Conversely, this means that a large eigenvalue on the main axis implies a strong relationship between most important environmental variable and the main complex gradient of change unless the gradient reflects a series of environmental variables. The latter is a highly improbable scenario in this case of a fairly homogenous environment through the deposition space and time. An eigenvalue that is as strong as the first axis of the DCA ordination performed herein (DCA1) (Table 5.4), indicates a strong relationship between the most important environmental variable and DCA1.

6.2 Ecological interpretation

Ecological interpretation of ordinations

A gradient in species composition which is as clear as DCA1 must be a result of significant changes in physical conditions. According to “the marine habitat classification for Britain and Ireland” by Connor et al. (2004), physical conditions that regulate habitats in a marine environment are: Substratum, topography, shading, tidal dependent zonation, wave action exposure, wave surge, scour, turbidity and siltation, tidal currents, salinity, temperature, oxygenation, hydrographic regime and light.

All of these factors may be time dependent under some circumstances, and a change in them will influence the environment.

- Substratum has been registered, and all fossils except superabundant *Chondrites* were collected on mudstones with homogenous particle size. Substratum is therefore not considered as a factor influencing the species composition.
- Topography and shading is probably not a significant factor influencing temporal changes in species composition, it needs more than some seven hundred thousand years to change topographic properties significantly.
- Tidal dependent zonation and wave action exposure (including wave surge, scour, turbidity and siltation) are probably not issues here, because sediments have been interpreted mainly as below storm wave level, and certainly below normal wave influence (Ribland Nilssen 1985; Harland 1978). If tidal dependent zonation or wave action had been an issue, it would be sea depth dependent.
- Tidal currents might change with changes in sea depth.
- The depth below storm wave level should provide conditions for stenohaline and stenothermal species. However, if the study area was a lagoon or any other landscape made by topography, these conditions might be influenced by a change in sea level even in deeper areas.
- Oxygenation is dependent of the circulation and the hydrographic regime. The water column might have very different nutrient and oxygen conditions above and under the circulation barrier made by stratification (Kaiser et al. 2005; Barnes 2004). A change in sea depth might vertically displace the stratification barrier, and thus provide an environment for new species. Anoxic conditions do not seem to be an issue, since fossils are abundant along the whole gradient.
- Light will locally correlate strongly with sea level changes.

All the factors above are either sea level dependent, or are not relevant for the species composition gradient extracted herein. Sea level is thus the most important environmental variable. This information combined with the high eigenvalue on DCA1 indicates a strong relationship between sea depth and DCA1, with increasing sea depths with decreasing DCA1 values.

A global drop in sea level during the time studied is generally recognized (Nielsen 2004; Hallam 1992), and this has also been identified locally (Ribland Nilssen 1985; Harland 1978). DCA1 and time should therefore correlate strongly. This is presented in Figure 5.7, with stratigraphy as an indicator of time. The relationship does not seem to be very strong, even though DCA1 scores are higher in the uppermost sediments. DCA1 scores are lowest in the middle stratigraphic level, illustrated by the red line in the figure.

This deviation from the prediction might be caused by two different circumstances:

- There are few quadrats in the area ordinated with lowest DCA scores. It might be a deviation due to stochasticity and insufficient amount of data.
- The relationship does correlate with sea level fluctuations, and might detect changes in sea level which are not detected in previous studies based on lithological evidence.

Sea depth itself rarely exerts direct control on the benthic communities; it is rather to be considered as a complex gradient composed of different environmental factors corresponding with sea depth as discussed above (Holland et al. 2001; Patzkowsky 1995). Indeed other factors as well might contribute to the sea depth complex gradient. Holland et al. (2001) have identified subtle biofacies in a formation lacking lithological evidence for environmental variation. The research was based on multivariate analysis, drawing the conclusion that the main gradient of community change corresponds with sea level fluctuations. This has later been supported by Scarponi and Kowalewski (2004) which have tested bathymetric gradients in fossil mollusk faunas of extant mollusk species by the use of multivariate methods. Results are calibrated with data from recent faunas, providing outstanding estimates for bathymetry. Calibration possibilities in Paleozoic benthos are limited. However, trophic level and way of feeding are known. As presented in Figure 6.1, the abundance of algae and photosynthesizing organisms' decreases with increased depth, while the abundance of animals increases.

The *Coelosphaeridium*, the *Mastopora*, and the *Leptaena* associations identified in Figure 5.3 and Figure 5.4 reflect subtle biofacies within the Fossum Formation. Based on general biological reasoning, these biofacies represent different environmental properties controlled by sea level fluctuations. There is an increasing number of both species and individuals of photosynthesizing organisms with increased DCA1 values (Figure 5.9). In the *Leptaena* association the surface is more or less completely covered with *Leptaena* brachiopods, while in the *Coelosphaeridium* association the surface is covered with primary producers. The evidence of such a strong correlation leads me to the conclusion that DCA1 is an index of sea level fluctuations.

Compared with terminology from Recent marine biology, as presented in Figure 6.1, the *Coelosphaeridium* association is interpreted as "lower infralittoral", the *Mastopora* association corresponds with "upper circalittoral", while the *Leptaena* association corresponds with "lower circalittoral".

Sedimentation rates were in general low in this area during the lower Upper Ordovician compared to conditions in recent British waters, making waters much more permeable for light. Sea depths corresponding to benthic regimes presented in Figure 6.1 may therefore be to shallow compared with the conditions studied here. New estimates of depth in benthic regimes and the corresponding associations identified herein are presented in Table 6.1. Values for the associations have been found in Hiscock (1996) and Kaiser et al. (2005), based upon knowledge of light conditions in clear waters and the level of storm wave influence. Depth values must be regarded as qualified estimates, rather than accurate calculations.

Table 6.1 Relationship between benthic regimes and fossil association, with estimates of sea depth.

Association	Regime	Sea depth
<i>Coelosphaeridium</i>	Lower infralittoral	80-50m
<i>Mastopora</i>	Higher circalittoral	200-80m
<i>Leptaena</i>	Lower circalittoral	>200m

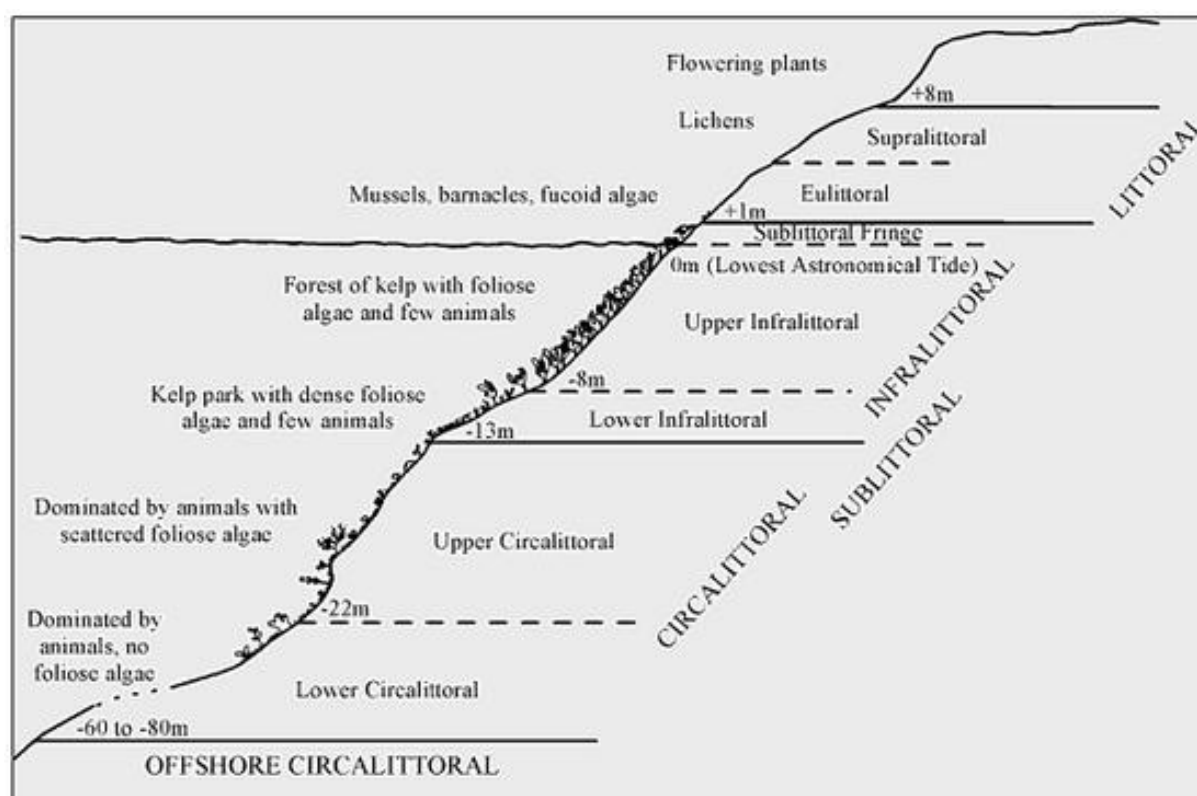


Figure 6.1: Relationship between trophic level and sea depth in recent benthic environments. The deepest areas are inhabited mostly by animals, while the shallowest areas are algae dominated. The depths presented in the figure are not valid for the Fossum formation due to different sedimentation environments. The figure is from Hiscock (1996).

Diversity

Diversity measurements have been done for each of the test squares in this study, measured with the Fisher Alpha diversity index. Most diversity indices can be considered as combination of number of species and evenness in distribution of species. This calculation might give the same index for very different properties of a community. Such measurements should therefore be interpreted with care. However, since superabundance for one species in a species rich community is not present here, the Fisher Alpha index is an appropriate diversity index. The only diversity measured is that of fossilized organisms. The diversity impact of non-fossilized non calcareous organisms is unknown, and such

organisms might very well fill niches occupied by calcareous organisms at other depths. Diversity is therefore not as accurate as for neontological studies, but might still reflect patterns similar to those observed in recent communities.

Diversity measurements are presented in Figure 5.8, which illustrates how the diversity index is unimodally distributed along DCA1. The trend is consistent with the “intermediate disturbance hypothesis”. Diversity is highest when disturbances are intermediate in intensity and frequency and lower when disturbances are at either extreme (Kaiser et al. 2005; Begon et al. 1998; Connell 1970). Intermediate disturbance interrupts succession progress, leaving patches with different succession states. This will conserve a varied environment containing different succession states (Begon et al. 1998; Connell 1970). Limitation in succession time also reduces community maturity, preventing less diverse communities of slow growing organisms with competitive advantages; a scenario which is especially prominent in communities of sessile organisms which compete for space (Connell 1970).

Shallow waters are often disturbed by storms, temperature changes, salinity fluctuations etc. Organisms in deep waters are offered more stable conditions and may over time develop into a mature community. Sea depth might in this way reflect a gradient from high to low disturbance. The diagram presented in Figure 5.8 reflects a unimodal relation between DCA1, interpreted as sea level, and diversity.

The diagram also show that test squares interpreted as the deepest have very low diversity. The scarcity of data might disturb the DCA, but this trend could also be result of succession, and reflect an undisturbed community, protected by the depth in which it is situated.

Diversity along bathymetric gradients has been discussed in many papers (Rex et al. 2005; Palmer 1994). Palmer (1994) has listed 120 different published explanations for trends in diversity.

Recent studies however, have suggested that there might be a unimodal relationship between energy/production and diversity, where high production often increases abundance of few species rather than the diversity (Rex et al. 2005; McClain et al. 2004) A unimodal relationship between diversity and production is quite common, though not universal (Rex et al. 2005). An energy/diversity relationship is a reasonable explanation for the diversity graph presented here, when DCA1 is interpreted as depth, which has decreasing amount of light. Rex et al. (2005) also point at a dramatic change in diversity below the permanent thermocline. Hence, the change in diversity can also be the result of strongly stratified Ordovician waters. This may result in increased species richness in the border areas between the two habitats, because species may permeate the border to some extent, creating an environment consisting of species from both habitats. This is often referred to as the edge effect.

This mid domain effect may also be influenced by geometrical properties of the data, which tend to always give a unimodal relationship between a true gradient and diversity (Colwell and Lees 2000). Colwell and Lees also point to bathymetric gradients as an example that gives a unimodal relationship in diversity. The above reasoning, although very general in nature, points to a series of depth dependent diversity relationships relevant for this case. Intermediate disturbance effects, the energy/diversity explanation and the geometrical explanation probably contribute to the bathymetric diversity gradient presented here, leaving the impact of the different factors for

uncertainty; in addition to a possible edge effect. All of the four explanations point to a depth related diversity gradient, which strengthens a bathymetric interpretation of the DCA1 axis from the ordination analysis.

***Leptaena* size analyses**

Leptaenas within the superabundance area, which is equal to the *Leptaena* association derived from the ordination analysis, are significantly larger and varies less in size than *Leptaenas* elsewhere. They therefore seem to have a larger tendency to achieve their maximal size, as well as fulfilling their life cycle in superabundant areas (Figure 5.10; Figure 5.11; Table 5.5). What seems to be a bimodal peak in the histograms is probably an artifact of the sampling method, where rounding off to closest integer numbers seems to have been preferred subconsciously during the field work.

Results are consistent with environments offering an optimal niche for *Leptaena* in superabundant areas. An optimal *Leptaena* niche could be the result of changes in environmental variables, as well as succession. They are probably exposed to fewer disturbances, with a more mature succession state as the result. *Leptaenas* are sessile organisms competing for space.

This gives a picture of a mature lower circalittoral community with few disturbances, low diversity with few animal species and no primary producers. Filter feeders do not need to compete for space with primary producers. The *Leptaena* association as a low diversity lower circalittoral community also fits neatly into the energy/diversity relationship posed by Rex et al. (2005) and McClain et al. (2004). The association might even have been situated below the permanent thermocline as posed by Rex et al. (2005).

Directional analysis

Directional analysis has already been discussed in the “*in situ* properties of the fossils” chapter, but only for the purpose presented there. Directional analyses give significant results for one main orientation of *Leptaena* and crinoid stems. Harland (1978) also studied paleocurrent relationships at this locality sedimentologically, and he interpreted the direction of currents as tidal movements up and down the shore. His study is from sediments deposited during a shallower period than the study object herein, namely the Steinvika Formation. Steinvika is the formation located above the Fossum Formation.

Directions herein are between 55° and 57° which is a northeasterly direction (Figure 5.2; Table 5.2). Harland has pointed out a northwesterly and southeasterly trend. It is expected that currents in a section deposited in depths mostly below storm wave basis and certainly below normal wave basis, are not affected by tidal movements on the shore. Directions herein are rather a result of an along-shore current in deeper waters that has a nearly normal angle to the tidal movements from the shallower sediments.

6.3 Sedimentological indicators of sea level

The stratigraphic log (Appendix 2) includes information on cross bedding, which is interpreted as a result of storm wave influences. Cross bedding appears in the stratigraphy in the upper part of the *Mastopora* association, but disappears before 700 cm in the stratigraphy. It reappears again above this level, together with increased carbonate contents in the sediments. Cross bedding is therefore not present in the *Leptaena* association, and supports the interpretation of increasing depth. The reappearance of cross bedding and limestone horizons in the overlying succession supports a transition to even shallower waters.

The paleogeography in the study area is interpreted to be a peneplanated partly submerged continent with no dramatic topography. An increase of sea level during deposition of sediments between 100 and 600 cm in the stratigraphy as interpreted from Figure 5.7, would thus lead to longer distance to land or shallow areas. If the rate of disturbances in the water is fairly constant, one would expect deposits from storms or other disturbances to be less frequent and thinner in the areas deposited during a drowning period than those deposited in a shallow period.

As a support for the sea depth relationship discussed herein, the lithological log (the total log is presented in Appendix 2) has been presented with a B-spline fit visualizing the decreasing trend in appearance of siltstones in the lower six meters of sediments (Figure 5.12). It has been tested with a logistic regression. The test was significant ($p < 0.001$; Figure 5.13) as expected. The relationship between a decreasing trend in amount of siltstones in Figure 5.12 and Figure 5.13 is consistent with the decrease in DCA1 values (Figure 5.7) compared with stratigraphy. Stratigraphical examination thus supports the depth interpretation of DCA1.

Nielsen (2004) has made a small scale sea level curve for the entire Ordovician. He does however not include the Fossum Formation in his stratigraphy. His age estimates also deviate from those presented in Owen et al. (1990). Owen et al. (1990) has placed the top of the Fossum Formation within the Frognerkilen Formation of Oslo-Asker and Ringerike, and at the base of the *Clingani* graptolite zone. This gives a good correlation with Nielsen's stratigraphy. Sediments which are studied here correspond with the time between the Keila Drowning Event and the Frognerkilen Lowstand Event. Uncertainties in exact time due to differences in sedimentation rates make it difficult to correlate exactly between Nielsen's curve and DCA1. However, there is a bimodal peak within the Keila Drowning Event. The second peak in this event may correspond to the drowning associated with the *Leptaena* association, with the Frognerkilen Lowstand event following above. Nielsen's sea level curve for the Ordovician is presented in Figure 6.2.

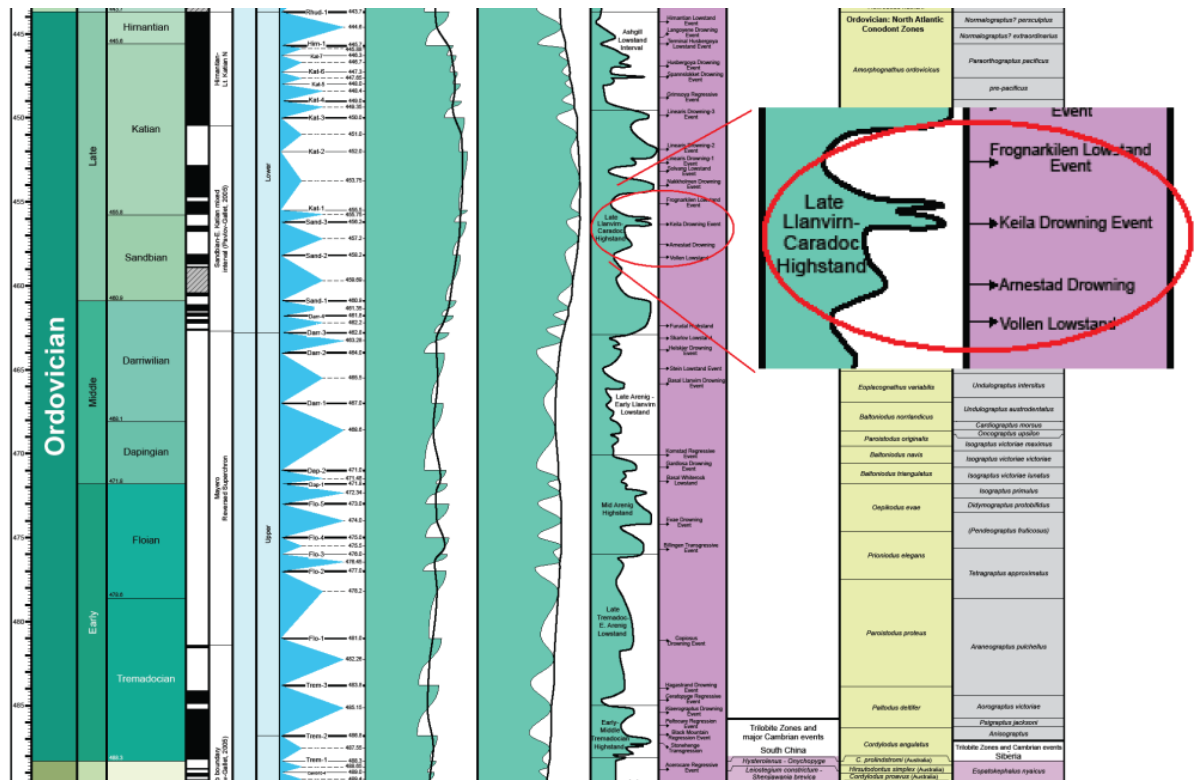


Figure 6.2: The Ordovician time scale with sea level curves, with the Keila Drowning Event and Frognerkilen Lowstand Event highlighted. The bimodal peak in the Keila Drowning Event might correspond to sea level fluctuations derived from DCA1 in Figure 5.7. This figure is taken from Ogg et al. (2008) with additional information from Haq and Schutter (2008)

7.0 Concluding remarks

7.1 Conclusions

- Data collected in this study are interpreted as representing *in situ* organisms, suitable for paleoecological investigations. They have not been subject to extensive transport during drowning events, and represent the biota of the locality when they were alive. A possible degree of allochthonous elements in strata deposited at shallower depths is a response to sea level fluctuations, and does not interfere with a sea level interpretation of ordination gradients.
- Gradients in species composition can be extracted with multivariate techniques which are well suited for this kind of data.
- One clear gradient in species composition has been extracted. Good correlations between gradients used with different methods give strong confidence in results.
- A high eigenvalue for the main gradient suggests a strong relationship between the gradient and environmental variables.
- An interpretation of the main gradient based upon recent habitat classification and ecological properties of the organisms, leads to the conclusion that sea level fluctuations are the main environmental component in this gradient. Sea level fluctuations are presented in Figure 5.7.
- This interpretation is supported by general ecological evaluation, as well as the diversity measurements, the presence of superabundant fossils, sedimentation patterns and previous research.

Results retrieved in this study build a picture of a benthic community transitioning from one state to another as the sea level changes. Namely from a diverse upper circalittoral environment with both animals and primary producers, through a less diverse lower circalittoral environment dominated by *Leptaena* to the infralittoral *Coelosphaeridium* association in the latest part of the succession.

7.2 Significance of results

Results presented in the present paper may be used for a deeper understanding of this particular paleoecological community. It may also contribute to general knowledge in both paleontology and ecology.

Of more specific significance are the methods used, and in particular the use of a species composition gradient as a small scale sea level proxy in the absence of good sedimentological evidence. A small-scale sea level estimation locally might be of great help in correlating and dating of sedimentary formations (sequence stratigraphy), or at least as a supplement to a traditional approach, especially when sedimentological/lithological evidence or trace fossils are absent.

A biological response to the sea level fluctuations and climate change is highly relevant in the debate on anthropogenic CO₂ emissions. All new parts of the puzzle might lead to better understanding of possible effects of increased CO₂ concentration in the atmosphere.

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Appendix 1: Species list and pictures

Table A.1:

Species

?Chasmops



Coelosphaeridium



Conulariida



Chondrites



Crinoid fragment



Crinoid stem



***Diplotrypa*, small**



***Diplotrypa*, large**



Echinospaerites



Gastropod



Strophomena



Leptaena



"Krogshavn" orthid



Mastopora



?Ogygiocaris



Platycoryphe



Rough Orthid





Small Orthid

Appendix 2: Stratigraphic log

Measured Section Field Form					
Location: Steinvika					
Date:		Name: Lars Qviller		Fossils presented herein are fossils of special interest. For total fossil distribution, see spindle diagram in figure 5.1 in the Results chapter.	
Fm./Strat. Unit: The Fossum Formation					
Depth (m)	Lithology	Sedimentary Structures		Description	
		Physical	Biogenic		
12				Siltstones and mudstones with cross bedding and without distinct shifting.	Coelosphaeridium association
11				Limestone	
10				Alternating siltstones and mudstones with cross bedding.	
9				Alternating siltstones and mudstones with cross bedding.	
8				Alternating siltstones and mudstones with cross bedding.	
7				Alternating siltstones and mudstones without cross bedding.	Leptaena association
6				Alternating siltstones and mudstones with cross bedding	
5				Alternating siltstones and mudstones without cross bedding.	The Mastopora association
4				Alternating siltstones and mudstones without cross bedding.	
3				Alternating siltstones and mudstones without cross bedding.	
2				Alternating siltstones and mudstones without cross bedding.	
1				Alternating siltstones and mudstones without cross bedding.	

Legend:

- Cross bedding
- Mudstone
- Siltstone
- Calcareous rock
- Leptaena
- Crinoid debris
- Chondrites
- Coelosphaeridium

Appendix 3: Ordination data

Species plot matrix

Test square	Stratigraphy	<i>Leptaena</i>	Crinoid_stems	<i>Diplotrypa</i>	<i>Coelosphaeridium</i>	<i>Platycoryphe</i>	Rough_orthid	Crinoid_fragments	Small_orthid	<i>Mastopora</i>	<i>Strophomena</i>	Orthid "krogshavn"	Echinospaerites	Total
5	1240	1	0	0	0	0	0	0	0	0	0	0	0	1
6	1240	0	0	1	42	0	0	0	0	0	0	0	0	43
9	1070	0	10	0	50	0	0	50	0	0	0	0	0	110
10	1070	0	2	0	0	0	0	0	0	0	0	0	0	2
11	1070	0	9	0	10	0	0	3	0	0	0	0	0	22
12	1070	0	1	0	17	0	0	4	0	1	0	0	0	23
14	1070	0	8	0	0	0	0	3	0	0	0	0	0	11
15	1070	0	5	0	26	0	0	39	0	0	0	0	0	70
19	710	64	0	0	0	0	0	0	0	0	0	0	0	64
20	710	97	0	0	0	0	0	0	1	0	0	0	0	98
21	710	66	5	0	0	0	0	0	0	0	0	0	0	71
22	710	39	6	0	0	0	0	3	0	0	0	0	0	48
23	710	6	4	0	0	0	0	2	0	0	0	0	0	12
24	710	10	10	0	0	0	0	29	0	0	0	0	0	49
25	340	0	1	0	0	0	1	1	0	0	0	0	0	3
27	320	8	3	6	0	0	0	11	4	5	1	0	0	38
28	415	2	0	1	0	0	1	0	0	0	0	0	0	4
29	420	14	1	2	0	0	0	0	0	0	0	0	0	17
30	440	6	2	0	0	0	0	0	2	2	1	0	0	13
31	320	2	2	1	0	0	0	0	0	0	0	0	0	5
33	320	3	8	0	0	0	0	7	1	1	0	0	0	20
34	340	7	0	0	0	1	0	0	6	0	0	0	0	14
35	320	2	1	1	0	1	0	1	0	0	0	0	0	6
36	605	8	5	1	0	0	0	0	0	2	2	0	0	18
37	45	31	4	0	0	0	0	1	0	0	1	0	0	37
38	95	0	0	2	0	0	0	0	0	0	1	0	0	3
39	95	2	1	0	0	0	0	0	2	0	1	0	0	6
40	95	0	0	2	0	0	1	6	0	0	1	0	0	10
41	340	1	23	3	0	0	1	54	6	5	4	0	0	97
42	340	7	5	2	0	0	0	33	4	2	0	0	0	53
43	340	5	3	2	0	0	0	10	0	0	0	0	0	20

44	1070	0	0	0	108	0	0	1	0	0	0	0	0	109
45	928	19	2	0	0	0	0	6	0	4	0	0	0	31
46	842	31	7	2	32	1	0	72	1	0	2	0	0	148
48	0	0	0	0	0	0	0	2	0	0	0	0	0	2
51	75	0	2	0	0	0	0	0	0	0	0	0	0	2
53	95	0	0	0	0	0	0	5	0	0	0	0	0	5
56	340	1	0	0	0	0	0	0	0	0	0	0	0	1
57	340	5	0	0	0	0	0	0	0	0	0	0	0	5
58	340	4	0	0	0	1	0	1	2	0	0	0	0	8
60	340	10	0	0	0	0	0	11	3	0	1	0	0	25
62	320	2	3	0	0	0	0	0	0	0	0	0	0	5
63	340	10	0	0	0	0	0	0	0	0	0	0	0	10
64	240	3	4	0	0	0	0	3	2	0	1	0	0	13
65	290	0	0	0	0	0	0	3	0	0	0	0	0	3
66	95	0	0	0	0	0	0	1	0	0	0	0	0	1
67	710	20	0	0	0	0	0	0	0	0	0	0	0	20
68	710	24	2	0	0	0	0	0	0	0	0	0	0	26
69	710	17	3	0	0	0	0	5	0	0	0	0	0	25
70	710	16	3	0	0	0	0	0	0	0	0	0	0	19
71	710	23	0	0	0	0	0	0	0	0	0	0	0	23
74	710	14	4	0	0	0	0	8	0	0	0	0	0	26
75	710	119	1	1	0	0	0	0	1	0	0	0	0	122
76	710	23	5	0	0	0	0	0	0	0	0	0	0	28
79	900	0	0	0	0	0	0	0	0	0	1	0	0	1
83	900	0	1	0	0	0	0	2	0	0	0	0	0	3
91	1070	0	0	0	9	0	0	0	0	1	0	0	0	10
93	1070	1	0	0	0	0	0	0	0	1	0	0	0	2
94	1070	0	0	0	1	0	0	0	0	0	0	0	0	1
L1	-39 meters	0	5	0	0	0	0	24	0	0	0	4	25	29
L2	-38 meters	0	38	2	0	0	0	14	0	0	0	0	13	54
L3	-40 meters	0	12	1	0	0	0	35	0	0	0	4	0	48
L4	-38 meters	0	5	0	0	1	0	0	0	0	0	0	1	6
L5	-40 meters	0	9	1	0	0	0	50	0	0	0	0	0	60
L6	-39 meters	0	10	0	0	0	0	13	0	0	0	0	12	23

Appendix 4: Cyclostratigraphic analysis

A stratigraphic log was retrieved by registering sediment type on a 1cm scale. Measurements were done with a measuring tape vertically on the stratigraphic horizons. This analysis was done as an attempt to correlate the stratigraphy with Milankovich cycles.

The sediments consisted of two main types of rock, namely siltstones and mudstones. The shifting between sediment types was tested for cyclicity with spectral analysis (Fourier transform and Walsh transform power spectra). Spectral analysis has been performed in PAST. Walsh transform power spectra was used because it is supposed to have better properties for binary data input (Negi et al. 1993; Weedon 1989).

Alternations in stratigraphy

The 600 centimetres of alternating sediments was analyzed with two spectral analyses, namely Walsh and Fourier transform analysis. Results from both analyses were consistent; however the most distinct pattern was retrieved from the Walsh Transform algorithm (Figure A4).

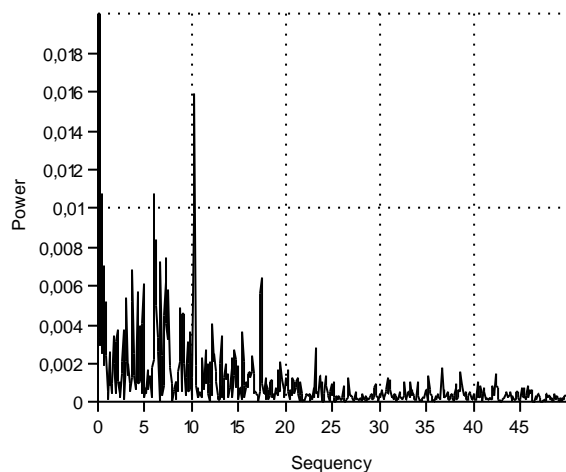


Figure A4: Walsh Transform diagram. Showing peaks in the spectrogram at 6.0, 10.2, and 17.4 sequences/meter (seq/m), with the peak at 10.2 seq/m as the most distinct, with a power of 0.016.

The analysis returned a diagram with prominent peaks in 6.0, 10.2 and 17.4 sequences per meter. The Walsh transform indicates a clear cyclic pattern. With a total age of the Fossum Formation of 13.5 million years and 255.5 meters thick formation, assuming constant sedimentation rates the sequences last approximately 8800 years, 5200 years and 3000 years.

The periods in astronomical cycles were shorter in the Paleozoic than they are today, due to a shorter distance between the earth and the moon. Berger et al. (1992) has investigated such cycles during the entire Phanerozoic, concluding with periods in obliquity and climatic precession from 35 to 54, 29 to 41, 19 to 23, and 16 to 19 thousand years. The periods for the Ordovician are presented in Table A3.

Table A4: Expected cycles in the left column, and detected cycles in the right column.

Periods in years according to Berger et al. (1992)	Detected cycles
16300,0	3000
19200,0	5200
30300,0	8800
36800,0	?

As we can see from Table A4, there is a large difference between cycles predicted by Berger et al. (1992) and the ones detected herein. One of the cycles is even missing. If there is a relationship, this is a subtle one that deserves lots of labour to interpret. Such clear tendency in cyclisity should be investigated, but this is a relationship that I have not prioritized in this M.Sc. study, and is therefore left for later studies.

References

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